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A Comparative Anatomical Study of Mandibular Structure in Bees[1] (Hymenoptera: Apoidea)

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ABSTRACT

Mandibular structures, particularly the ridges and grooves of the outer and inner surfaces, were investigated and illustrated for all major groups of Apoidea. A nomenclature is provided for these structures, and homologies among apoid groups are indicated. A basic mandibular type is found among sphecoid wasps, all short tongued families of bees, and also the Anthophoridae and Fideliidae. Various modifications are found within some of these groups, such as the parasitic anthophorids, the Hylaeinae and Xeromelissinae, and the Xylocopinae. Markedly modified mandibles characterize the Megachilidae and the Apidae.

INTRODUCTION

The taxonomic literature on bees contains many descriptions and illustrations emphasizing the distal parts of mandibles —the apical margins and teeth. These are features whose form is easily seen if the mandibles are open and whose functions are sometimes obvious, e.g., cutting edges

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on mandibles of females of leaf-cutter bees (*Megachile*) or multidentate apices of mandibles of those anthidiine bees (e.g., *Anthidium*) that makes their nests with plant hairs. The present paper is not primarily concerned with these features, but deals instead with the surfaces, ridges, and grooves of the mandible, i.e., the body of the mandible. In general, the mandibular body is more conservative than the apical teeth, showing less diversity among species and related genera. A few authors have used the ridges and grooves taxonomically, but in the absence of an overview, no homologies among diverse groups have been apparent and no standard terminology exists.

The object of the study here reported was to establish homologies and terminologies for the parts of the mandible, to facilitate their study, and to look for characters that might illuminate the relationships among major groups of bees.

MATERIALS

The mandibles of many bees were examined in the course of this study. Generally, mandibular structures are better developed in females than in males; detailed analysis was therefore based on females except as noted. From among the many mandibles studied, those of the species listed in Table 1 were selected as representative of most of the variation in the pattern of ridges and grooves and many of them were diagrammed (outer and inner views) as indicated in the table by references to figures.

Species with bizarre swellings or projections are excluded from those illustrated, for they do not contribute to the understanding of the basic structures. However, once the latter are identified, it is often possible to see that a given projection is an elaboration of a particular ridge or interspace.

Letters corresponding to the abbreviations in the figures are given after the names of the structures, where the word or expression is defined in the following section and also in a tabular summary at the end of that

TABLE 1

SPECIES STUDIED.

FAMILY COLLETIDAE
- Subfamily Colletinae
  - *Colletes inaequalis* (Fig. 2)
  - *Leioproctus herbsti*
  - *Callomelitta antipodes* (Fig. 3)
- Subfamily Diphaglossinae
  - *Diphaglossa gayi* (Fig. 4)
  - *Ptiloglossa guinnae*
- Subfamily Hylaeinae
  - *Hylaeus rugosulus*
  - *Amphylaeus morosus* (Fig. 5)
- Subfamily Xeromelissinae
  - *Chilicola ashmeadi* (Fig. 6)
- Subfamily Stenotritinae
  - *Ctenocolletes smaragdinus*

FAMILY HALICTIDAE
- Subfamily Halictinae
  - *Halictus ligatus, quadricinctus* (Fig. 7)
  - *Lasioglossum imitatum, lustrans, texanum, zephyrum*
  - *Pseudaugochloropsis graminea*
  - *Augochlora pura*
  - *Megalopta genalis*
- Subfamily Nomiinae
  - *Nomia melanderi*
- Subfamily Dufoureinae
  - *Dufourea marginata*
  - *Systropha curvicornis*

FAMILY ANDRENIDAE
- Subfamily Andreninae
  - *Andrena accepta* (Fig. 8), *illinoiensis*
- Subfamily Panurginae
  - *Panurginus occidentalis* (Fig. 9)
  - *Panurgus calceatus*
  - *Psaenythia bergi*
  - *Perdita chihuahua*

FAMILY OXAEIDAE
  - *Protoxaea gloriosa* (Fig. 10)

FAMILY MELITTIDAE
- Subfamily Melittinae
  - *Melitta leporina* (Fig. 11)
- Subfamily Dasypodinae
  - *Dasypoda panzeri*
- Subfamily Macropidinae
  - *Macropis labiata*
- Subfamily Ctenoplectrinae
  - *Ctenoplectra fuscipes*

TABLE 1—(*Concluded*)

FAMILY ANTHOPHORIDAE
- Subfamily Anthophorinae
  - *Exomalopsis zexmeniae*
  - *Tapinotaspis coerulea*
  - *Ancyloscelis apiformis*
  - *Diadasia enavata*
  - *Melitoma segmentaria*
  - *Anthophora occidentalis* (Fig. 12)
  - *Clisodon terminalis* (Fig. 13)
  - *Svastra atripes* (Fig. 14)
  - *Melissodes agilis*
  - *Centris poecila* (Fig. 15)
  - *Ericrocis lata* (Fig. 16)
  - *Mesoplia garleppi*
  - *Thyreus ramosa* (Fig. 17)
  - *Xeromelecta californica*
- Subfamily Nomadinae
  - *Nomada annulata* (Fig. 18)
  - *Triepeolus concavus*
  - *Biastes brevicornis* (Fig. 19)
- Subfamily Xylocopinae
  - *Macrogalea candida* (Fig. 20)
  - *Allodape mucronata* (Fig. 21)
  - *Ceratina dupla* (Fig. 22)
  - *Manuelia gayi* (Fig. 23)
  - *Xylocopa virginica* (Fig. 24)

FAMILY FIDELIIDAE
  - *Fidelia villosa* (Fig. 25)
  - *Neofidelia profuga* (Fig. 26)

FAMILY MEGACHILIDAE
- Subfamily Lithurginae
  - *Lithurge gibbosus* (Fig. 29)
- Subfamily Megachilinae
  - *Paranthidium jugatorium*
  - *Dianthidium ulkei*
  - *Callanthidium illustre*
  - *Anthidiellum notatum* (Fig. 27)
  - *Anthidium manicatum* (Fig. 28)
  - *Parevaspis carbonaria*
  - *Euaspis abdominalis*
  - *Chelostoma fuliginosum*
  - *Heriades carinatus*
  - *Osmia lignaria, subaustralis, subfasciata*
  - *Hoplitis albifrons* (Fig. 30; male, Fig. 31)
  - *Creightonella frontalis* (Fig. 32)
  - *Megachile albitarsis* (Fig. 33), *frugalis*
  - *Chalicodoma exilis* (Fig. 34)

FAMILY APIDAE
- Subfamily Meliponinae
  - *Meliponula bocandei* (Fig. 35)
  - *Trigona beccarii, braunsi, capitata* (Fig. 36), *chanchamayoensis, cupira, erythrea, mexicana*
  - *Dactylurina staudingeri*
  - *Lestrimelitta limao*
  - *Melipona fasciata*
- Subfamily Apinae
  - *Apis mellifera* (queen, Fig. 37; worker, Fig. 38)
- Subfamily Bombinae
  - *Euplusia violacea* (Fig. 39)
  - *Euglossa cordata*
  - *Eulaema dimidiata*
  - *Exaerete smaragdina* (Fig. 40)
  - *Bombus americanorum* (Fig. 41)
  - *Psithyrus variabilis* (Fig. 42)

section. Figure 1 illustrates certain structures not labeled in the remaining figures, but most ridges and grooves are labeled on all the figures where they appear. To avoid crowding the illustrations, structures along the upper and lower mandibular margins are minimally labeled. For example, in most of the illustrations the distal part of the adductor ridge, where it appears on the outer mandibular surface below the condylar groove, is not labeled. Structures on the upper mandibular margin such as the upper carina are ordinarily labeled on only one rather than both of the drawings of each mandible.

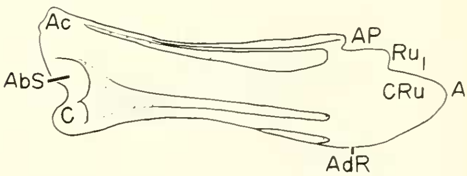


FIG. 1. Outer view of mandible of *Diphaglossa gayi*, female, with labels for structures not identified in other illustrations. For abbreviations see Tables 2 and 3.

Dots on the drawings indicate the areas with hairs. The meanings of the abbreviations are indicated in Tables 2 and 3.

Most of the terminology is new for this paper but (where practical) terms are those used by Michener (1944) and Eickwort (1969).

BASIC STRUCTURE AND TERMINOLOGY

For purposes of terminology, the mandible is considered to lie in a horizontal position (as when it is closed), so that it has upper and lower margins separating the inner and outer surfaces. Eickwort (1969) considered the mandible to project downward and to have anterior and posterior margins, but our assumptions seem more practical to us.

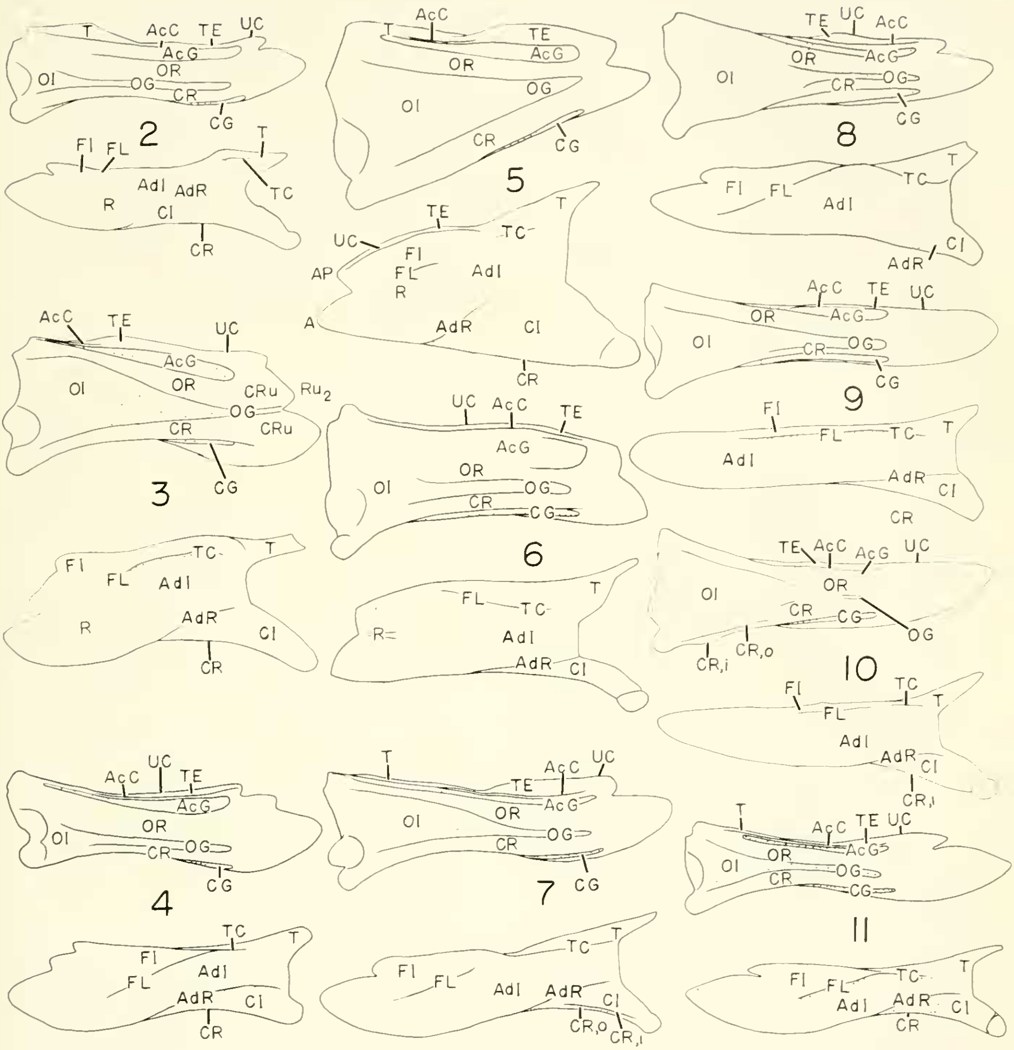
Mandibular Base: The base of the mandible is attached to the head capsule at the large and irregularly round mandibular socket between the lower end of the eye and the proboscidial fossa. In this socket the mandible can rock only in one plane, because of the double articulation consisting of the small anterior *mandibular acetabulum* (Ac), fitting over a condyle near the lower lateral angle of the clypeus, and a large posterior *mandibular condyle* (C), fitting into an acetabulum in the cranium below the eye. The line between these two articulations is the *articular axis,* about which the mandible rocks.

The outer margin of the mandibular socket is only moderately deviant from the articular axis. A small bulge in the outer margin of the mandibular base, a short distance in front of the mandibular condyle, is the *abductor swelling* (AbS) to which the *apodeme of the abductor muscle* is attached. Opening of the mandibles requires little power and the abductor swelling, as might be expected, is not far lateral to the articular axis; it provides no great mechanical advantage.

The main work of mandibles, i.e., biting, excavating soil or wood, and the like, requires strength in closing the mandibles. The inner margin of the mandibular socket is accordingly far mesal to the articular axis and the inner margin of the mandibular base is swollen to form the *adductor convexity,* sometimes called the adductor angle. To this convexity, far mesad from the articular axis and providing considerable mechanical advantage, is attached the *apodeme of the adductor muscle.* The whole inner basal mandibular surface is involved in the adductor convexity, while only a small local area forms the abductor swelling. The summit of the convexity is usually flattened and lies between the basal part of the adductor ridge and the trimmal carina (see below).

Mandibular Surfaces: If an imaginary "plane" through the articular axis were extended toward the mandibular apex, curving and sometimes twisting with the curvature of the mandible so that the maximum area of the plane is internal, i.e., inside the mandible, then the lines of intersection of the plane with the mandibular surface will separate the *outer surface* of the mandible from the *inner surface.* The outer surface is ordinarily gently convex, never far from this imaginary plane. The inner surface, commonly concave distally, is strongly convex basally, forming the adductor convexity. The lines along which the imaginary plane intersects the mandibular surface are the *lower margin* and the *upper margin* of the mandible. The details of the intersection of the plane with the mandibular surface vary, so that certain structures cannot be unhesitatingly attributed to one or the other surface.

The adductor convexity is often so large that, for the basal half of the mandible, the upper (or anterior) slope of the convexity could be considered as an upper (or anterior) mandibular surface, commonly beveled to pass the clypeal and labral margins when the mandibles are being



Figs. 2-11. Outer and inner views of mandibles of female Colletidae, Halictidae, Andrenidae, Oxaeidae, and Melittidae. For species names see Table 1; for abbreviations see Table 2 and 3.

closed. Likewise, for the basal part of the mandible, the lower or posterior slope of the adductor convexity could be regarded as a lower (or posterior) mandibular surface. Because upper and lower surfaces are not evident distally, it seems simplest not to use these terms, but to consider both as parts of the inner surface.

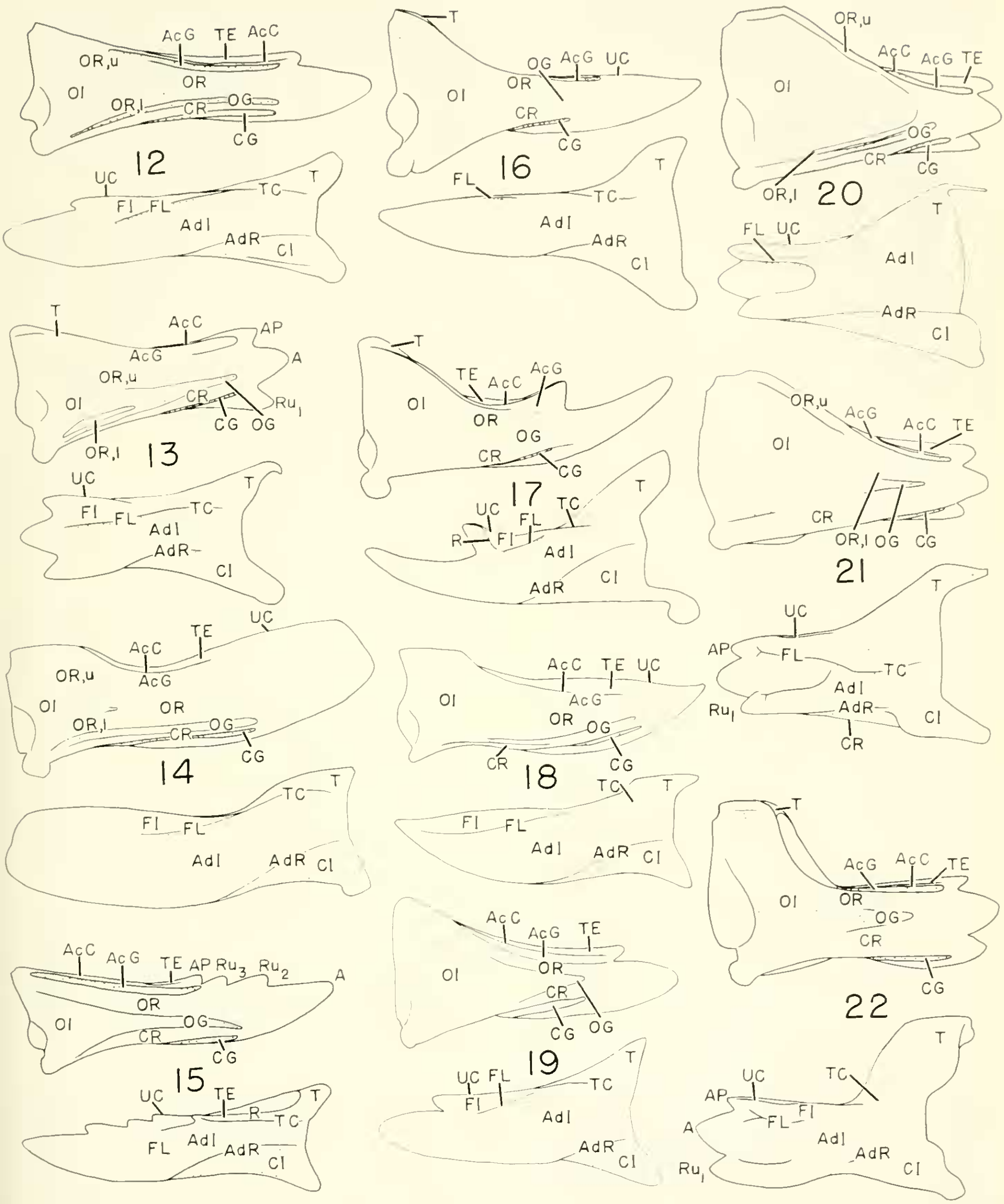
Outer Surface: Seen from the outer side, many bee mandibles have a preapical tooth (subapical tooth of Eickwort, 1969; Michener, 1944, etc.) on the upper margin; this tooth and the area basal to it are the pollex (thumb) while the remainder of the mandible is termed the rutellum (mitten). (For further details see below.) The outer surface of the mandible usually has several longitudinal, elevated areas or ridges that are normally smooth and hairless. They fuse toward the apex of the mandible to form a smooth surface, the *cap of the rutellum* (CRu). Between the ridges are grooves, almost always bearing hairs. Commonly, one groove (outer) is broadened basally, forming a more or less flat, non-elevated, hairy area that cannot reasonably be called a groove and is therefore called an interspace. Another groove (acetabular) in some bees (especially Megachilidae) is broadened apically to form an interspace that often contains longitudinal ridges which are probably secondary, not homologous to any of the more universal or primary, named ridges.

The lower margin of the mandible basally and sometimes apically is formed by the *condylar ridge* (CR) which arises near the mandibular condyle and extends toward the apex of the mandible, ultimately joining the cap of the rutellum. Usually, however, in the distal half of the mandible, the adductor ridge from the inner surface of the mandible comes into view below the condylar ridge, so that the lower margin of the mandible is formed distally by the adductor ridge, which also merges with the cap of the rutellum apically. Occasionally, as in *Halictus quadricinctus* and *Bombus,* the condylar ridge consists of two (even three) ridges with a hairy groove between them; one is clearly on the outer mandibular surface (CR, o) while the other is often on the lower margin or almost onto the inner surface (CR, i).

Above the condylar ridge and typically parallel to it is the piliferous *outer groove* (OG) which usually expands basally to form the broad, hairy *outer interspace* (OI) (but see below). Rarely, as in *Euplusia,* the distal part of the outer groove is divided, forming an upper and lower outer groove (OG, u; OG, l). Alternatively, elevation of all but marginal areas of the outer interspace may divide the median and basal parts to form upper and lower outer grooves, as in *Bombus* and *Psithyrus.*

Above the outer groove is the commonly broad and gently convex *outer ridge* (OR) (outer diagonal ridge of Eickwort, 1969) which distally is separated by the outer groove from the condylar ridge, and which merges distally into the cap of the rutellum. The outer ridge commonly occupies the median part of the outer surface of the mandible. Basally, the outer ridge usually curves upward (hence Eickwort's term, diagonal ridge) so that when complete, its base is near the acetabulum. When there is more than one base, this one is termed the upper root (OR, u). Sometimes, as in *Diphaglossa,* the upper root of the outer ridge is broad, so that its base occupies the space between the acetabulum and the abductor swelling; alternatively, the outer ridge may fade away basally into the outer interspace, the base of the upper root being represented, if at all, by an elevation just distad from the acetabulum and not connected to the distal part of the ridge. Other roots of the outer ridge are relatively rarely developed. Sometimes the ridge has a lower basal ramus or root (OR, l) extending toward the condyle (e.g., *Macrogalea, Anthophora*) or a median root (OR, m) extending toward the abductor swelling (e.g., *Chalicodoma*). In these cases, which are very similar to one another and probably represent the same development, the outer interspace lies between the two roots of the outer ridge. The outer ridge is so named because of its position; its basal connections are variable and not appropriate for purposes of naming the ridge.

When the outer ridge has lower or median roots, the outer groove is narrow to the base of the mandible and cannot



Figs. 12-22. Outer and inner views of mandibles of female Anthophorinae, Nomadinae, and Xylocopinae in the Anthophoridae. For species names see Table 1; for abbreviations see Tables 2 and 3.

expand into the outer interspace. An alternative interpretation would be that such roots are really formed by duplication of the condylar ridge. Examination of mandibles like those of *Anthophora* or *Clisodon,* however, show that the apex of the outer groove is in the same position as in most bees, and the extra ridge arises from the preapical part of the outer ridge. Mandibles like those of *Allodape* and *Xylocopa* show intermediate stages in development of lower roots.

Rarely, the distal part of the outer ridge may be deeply bifid, forming upper and lower branches (OR, d; OR, v) as in *Bombus*.

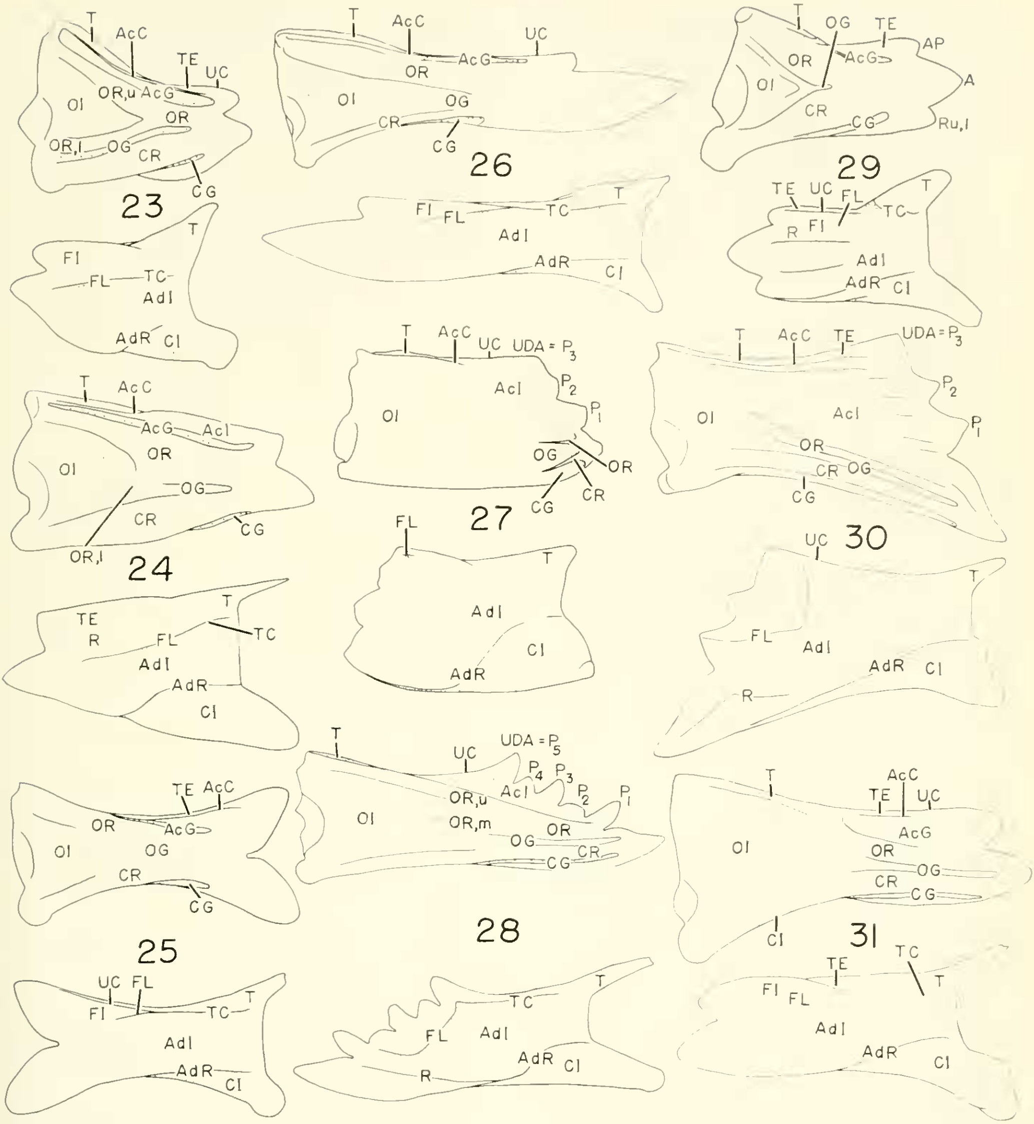
Above the outer ridge is the piliferous *acetabular groove* (AcG) (outer anterior groove of Eickwort, 1969), which arises distal to the acetabulum and extends toward the distal margin of the mandible. It usually fades away near the base so that the outer ridge (or its upper root) fuses with the acetabular carina basally. It ordinarily terminates before the distal margin of the mandible, and more or less separates the *pollex*, which usually forms the upper preapical mandibular tooth or margin, from the rest of the mandible (as seen from the outer surface), the *rutellum*. Thus, it does not end in the cap of the rutellum as do the grooves below it on the outer surface. [The rutellum and pollex are not separable on the inner, mandibular surface except by the notch on the distal margin in most species. Eickwort (1969) believed that the fimbriate line separates the pollex from the rutellum (our terminology) on the inner surface of the mandible, but this is ordinarily not the position of the fimbriate line.] Above the acetabular groove is the *acetabular carina* (AcC), a usually sharp ridge which arises near the acetabulum and extends distally toward the apex of the pollex. On the basal part of the mandible, the acetabular carina and the outer ridge are sometimes completely fused. This appears to be the case, for example, in male *Hoplitis* and in *Megachile* and *Chalicodoma*.

In some bees (Megachilidae, Apidae) the distal part of the mandible, above the outer ridge, is expanded apically as a broad space between the distal parts of the outer ridge and the acetabular carina. This space constitutes, or is occupied by, the acetabular groove in slender mandibles, but that term is inappropriate for a broad space, especially when there are several secondary ridges or possibly branches of the outer ridge in the area. This area is therefore called the *acetabular interspace* (AcI).

The acetabular carina may be the upper margin of the mandible. If not, the space and carina commonly narrowly visible above the acetabular carina have their principal connections with the inner mandibular surface and are described in the next section.

In some megachilid bees a striking feature is the *outer premarginal fimbria*, which arises from the *outer premarginal impressed line* (OIL). The fimbria or line roughly parallels the distal margin of the mandible across the acetabular interspace, but is absent in the region of the apex proper, i.e., on the cap of the rutellum. In the Meliponinae, there are no ridges on the outer mandibular surface or only the acetabular carina, but an *oblique groove* (OG) extends from near the acetabulum toward the mandibular apex. It seems likely that, near its base, the oblique groove is the acetabular groove, but distally it must be a secondary groove, for it goes toward the mandibular apex and has a branch going to the lower margin of the mandible. No such pattern occurs in the mandible of other bees.

Inner Surface: Arising on the adductor convexity is the *adductor ridge* (AdR). This ridge, the basal part of which is often not hairless and shining like ridges of the outer surface, follows a characteristic course, curving downward in the median part of the mandible toward the lower margin; thereafter it extends distally, commonly forming or being very near to the lower mandibular margin. This distal part of the adductor ridge was called the outer posterior ridge by Eickwort (1969). The



Figs. 23-31. Outer and inner views of mandibles of female (except for Fig. 31) Xylocopinae in the Anthophoridae, Fideliidae, and Megachilidae. For species names see Table 1; for abbreviations see Tables 2 and 3.

interval above the adductor ridge distally on the outer surface of the mandible, separating it from the condylar ridge, is the *condylar groove* (CG) (outer posterior groove of Eickwort, 1969). Basally, this interval is on the inner surface of the mandible and, because of the curvature of the adductor ridge, the interval becomes the broad lower surface or slope of the adductor convexity, i.e., the *condylar interspace* (CI).

Above the adductor ridge on the inner mandibular surface is the rather broad *adductor interspace* (AdI). This interspace is the median zone of the inner mandibular surface and is delimited above by the fimbriate line and trimmal carina.

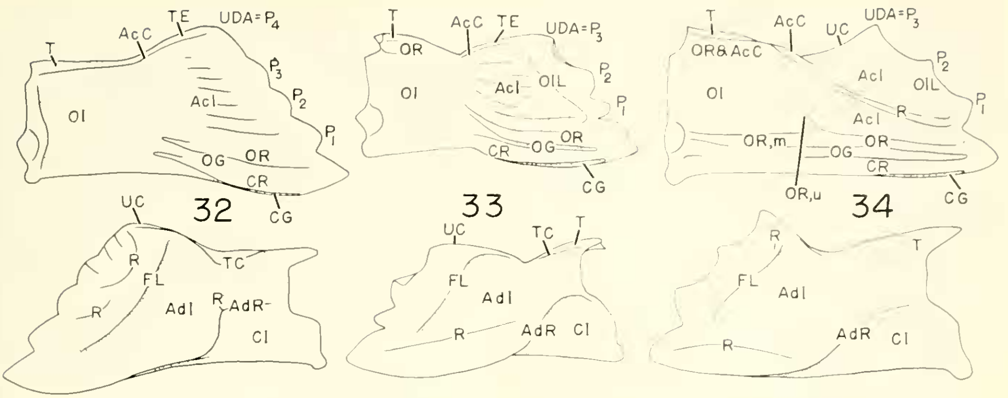
The *trimmal carina* (TC), sometimes

merely a ridge basally, arises on the upper surface of the adductor convexity and separates the basal part of the adductor interspace from the often flat *trimma* (T), a special basal mandibular area which is usually smooth and often bears some short, presumably sensory hairs and which slopes toward the upper margin of the mandible and passes the clypeal and labral margins when the mandible is being closed. The trimma forms the upper surface or slope of the adductor convexity and extends to the acetabulum; toward the outer mandibular surface it is limited by the acetabular carina if the latter extends far enough basally; if not, it is limited by the upper edge of the basal root of the outer ridge, which is probably fused with the base of the acetabular carina. The trimmal carina commonly extends distally to about the middle of the mandible. From there, it sometimes continues uninterruptedly as the *upper carina* (UC) of the distal part of the mandible, which usually forms the upper margin of the pollex. The interval between the acetabular carina and trimmal and upper carinae, basally the broad trimma, tapers distally to form a slender *trimmal extension* (TE) on the pollex. This is not a piliferous groove but a smooth area, as is the trimma.

Sometimes merging with the distal end of the trimmal carina and curving distally, often obliquely across the inner surface of the mandible, is the *fimbriate line* (FL). This is the line on which the often elevated upper part meets the often depressed median part of the inner mandibular surface. Sometimes the line is a ridge or a carina (the *fimbrial carina*), more often simply a step between two levels. The fimbriate line is usually marked by a series of hairs along its lower margin, hence its name; these hairs constitute the *inner fimbria*. The space between the fimbriate line and the upper carina is the *fimbrial interspace* (FI). It disappears basally where the upper carina and fimbrial ridge approach one another or unite, but distally it may expand to form the whole upper distal part of the concave inner surface of the mandible. In those bees (especially the Megachilidae) in which the mandibles are broad distally due to the expansion of the condylar interspace on the outer surface, an effect on the inner surface is that the fimbriate line becomes very oblique, even parallel to the distal margin of the mandible. The point where it fuses with or approaches the upper or trimmal carinae moves distad, often quite close to the upper distal angle of the mandible, thus essentially eliminating the fimbrial interspace.

The inner fimbria sometimes arises from a weak groove, called the inner anterior groove by Eickwort (1969), but it is ordinarily depressed only relative to the space above it and not relative to the space below it. Hence we have not used the word groove for it. When the fimbriate line is carinate, the carina may overlap the bases of the fimbrial hairs, which therefore emerge from behind the carina.

Relations among the trimmal carina, the upper carina, and the fimbriate line vary. Sometimes the three do not meet. Sometimes all three meet, forming a single Y-shaped system. Sometimes the trimmal carina continues uninterruptedly as the upper carina, with no connection to the fimbriate line. Sometimes the trimmal carina continues uninterruptedly as the fimbriate line without connection with the upper carina. Under these circumstances, there seems to be no alternative to three separate terms for the three structures. It may be, however, that the trimmal carina and fimbriate line constitute a single basic structure, sometimes interrupted medially, to which the upper carina is sometimes joined. This suggestion is based on the fact that the trimmal carina, like the fim-



Figs. 32-34. Outer and inner views of mandibles of female Megachilidae. For species names see Table 1; for abbreviations see Tables 2 and 3.

briate line, typically has a row of hairs along its lower margin. In fact, when the carina is weak or absent, its location is sometimes indicated by the row of hairs; the same is sometimes true of the fimbriate line.

Distal Margin: The distal or apical margin of the mandible varies from a single, narrowly rounded or pointed tip to a long, simple to multidentate edge. The *apex* (A), the distal extremity of the cap of the rutellum, is the part of the mandible farthest from the base and except in most Lithurginae and Xylocopinae and in *Clisodon* in the Anthophorinae, it forms the tooth that is a continuation of the lower margin of the mandible, often called the first tooth and here recognized as the first tooth of the rutellum. In some bees (e.g., *Panurginus*) there are no teeth, i.e., the mandible is simple and toothless.

In many bees there is a preapical tooth, the *apex of the pollex* (AP), on the upper margin. In such cases the mandible is often called bidentate, and the apex and preapical tooth constitute the distal margin.

In some bees such as *Centris*, the distal margin of the rutellum above the apex and below the pollex bears one to several teeth, the *upper teeth of the rutellum* (Ru_2, Ru_3, etc., Ru_1 being the apex). In some (most Lithurginae and Xylocopinae and *Clisodon*), there is a rutellar tooth below the apex and formed from the end of the adductor ridge. This is the *lower tooth of the rutellum* (Ru, l). When it is present, the distal margin of the mandible is tridentate, with the median tooth (mandibular apex) longest and with the lower tooth of the rutellum below it and the similarly shaped apex of the pollex above it.

In most female Megachilinae and to a lesser degree in some aphids, the distal margin of the mandible is elongate, because the region of the pollex is expanded distally to form two to several *teeth of the pollex* (P_1, P_2, etc.) or an edentate margin. The upper end of this margin or the uppermost tooth is the *upper distal angle* (UDA) or simply the upper angle (inner angle of much taxonomic work; we have avoided this term because it is not on the inner surface of the mandible).

Summary and Abbreviations: To summarize and organize the terminology, the longitudinal ridges, grooves, and interspaces are listed in Table 2, starting with the condylar ridge and proceeding upward on the outer surface of the mandible and continuing around the upper margin and downward on the inner surface. Distal structures that are, or may be, continuations of basal structures are indented below the name of the basal structure. In-

TABLE 2

Ridges, grooves and interspaces.

condylar ridge	CR
(when compound or additional ridges, outer and inner)	o, i
outer interspace	OI
outer groove	OG
(when compound, upper and lower)	u, l
outer ridge	OR
(upper median, and lower roots of outer ridge)	u, m, l
(upper and lower distal branches)	d, v
acetabular groove	AcG
acetabular interspace	AcI
acetabular carina	AcC
trimma	T
trimmal extension	TE
trimmal carina	TC
fimbriate line	FL
upper carina	UC
fimbrial interspace	FI
adductor interspace	AdI
adductor ridge	AdR
condylar interspace	CI
condylar groove	CG

dented items in parentheses are subdivisions of major structure.

Other special terms used are italicized in the preceding account. Those whose abbreviations are used in the illustrations are listed in Table 3.

TABLE 3

Other mandibular structures.

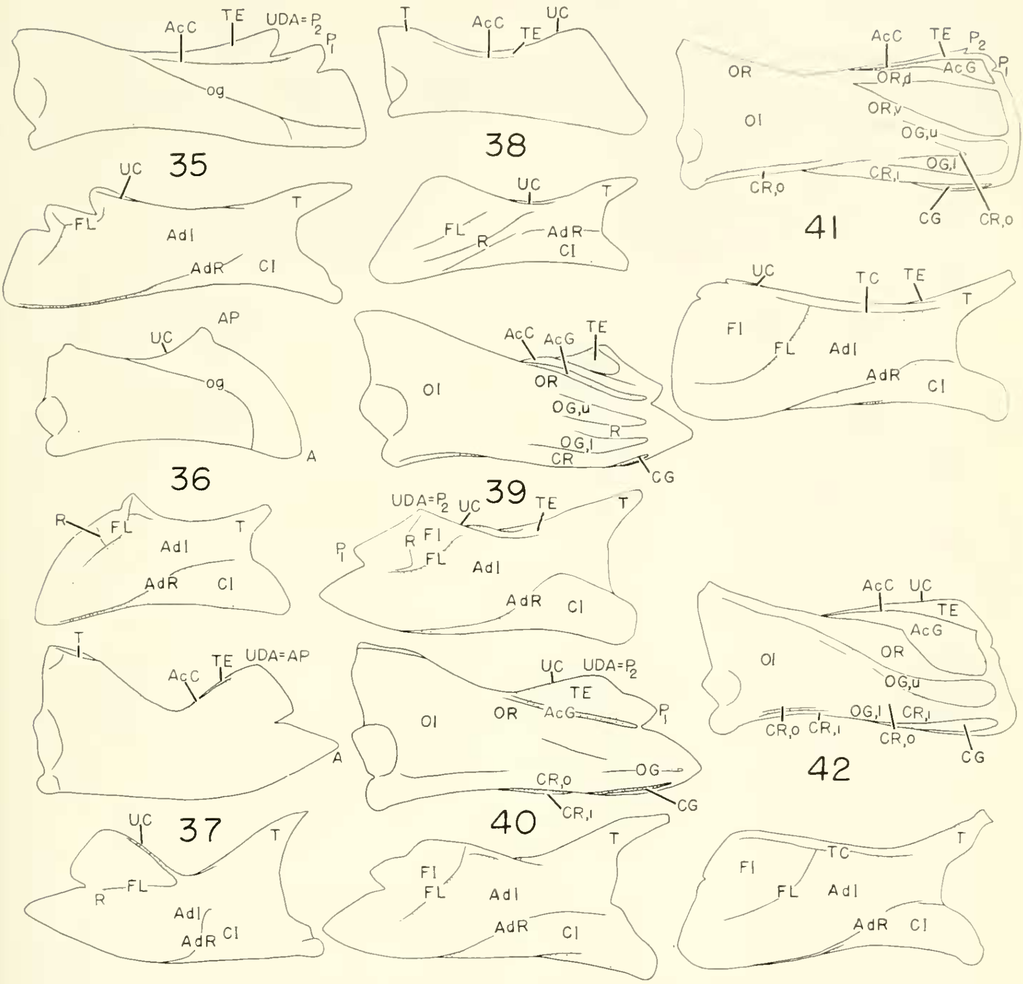
mandibular acetabulum	Ac
mandibular condyle	C
abductor swelling	AbS
apex (=1st tooth of rutellum)	A
upper teeth of rutellum	Ru_2, Ru_3, etc.
lower tooth of rutellum	Ru, l
cap of rutellum	CRu
teeth of pollex	P_1, P_2, etc.
apex of pollex (commonly preapical tooth)	AP
unnamed "secondary" ridges in certain genera or species	R
outer premarginal impressed line (Megachilidae)	OIL
upper distal angle (Megachilidae, Apidae)	UDA
oblique groove (Meliponinae)	og

COMPARATIVE STUDY

The Ancestral Type of Mandible: In a large group of ground-nesting bees, the mandibles are rather slender, usually with all or most of the structures listed in the preceding section in readily recognized form. Such mandibles occur in the Colletinae (Figs. 2, 3), Diphaglossinae (Fig. 1), Stenotritinae, Halictidae (Fig. 7), Andrenidae (Fig. 8), Oxaeidae (Fig. 10), Melittidae (Fig. 11), Anthophorinae (Fig. 12) and Fideliidae (Fig. 26).

Mandibles of this type occur also among sphecoid wasps. For this reason we consider them as ancestral among bees. Considerable variation occurs, however, among such mandibles. Some unusual and presumably derived features of certain mandibles in this group of bees are described below.

Colletid groups such as the Paracolletini (*Leioproctus* spp.), Diphaglossinae and Stenotritinae have rather ordinary mandibles. In *Colletes* (Fig. 2) and *Ptiloglossa* the adductor ridge fades out medially so that the basal part, on the adductor convexity and distal to it, is not clearly connected to the distal part along the lower margin of the distal half of the mandible. A continuation of the basal part extends distally, however, toward the mandibular apex, as a broad, secondary, longitudinal median ridge in the adductor interspace, a special and doubtless derived ridge not found in most other bees. A similar secondary ridge is weakly developed in *Callomelitta.* The latter genus is unusual for having the rutellum divided to form two teeth, a modification possibly associated with nesting in wood instead of soil.



Figs. 35-42. Outer and inner views of mandibles of female Apidae. For species names see Table 1; for abbreviations see Tables 2 and 3.

Halictids show only limited diversity in mandibular structure. In *Halictus quadricinctus,* but not in related bees such as *H. ligatus* and *Lasioglossum,* an inner condylar ridge lies just beneath the basal part of the lower mandibular margin and extends from near the condyle to the marginal part of the adductor ridge, leaving a pilose groove just behind the usual (outer) condylar ridge. Some wood-nesting halictids have slightly modified mandibles. Thus, *Augochlora pura* has the trimmal extension irregularly shaped and *Megalopta genalis* has the same feature and in addition two large teeth on the inner mandibular surface. These seem to be enlargements of the fimbrial carina, since there are a few hairs, more or less in line with those along the trimmal carina, above each of the teeth. In the Nomiinae (*Nomia*) and Dufoureinae (*Dufourea, Systropha*), the mandibles are ordinary and the fimbriate ridge is a mere change in level (depressed below the line), with no hairs in *Systropha.*

Andrena accepta and, to varying degrees, other species of *Andrena* are unusual in having the adductor ridge directed downward almost from its base so that the condylar interspace is very short and the condylar groove correspondingly long.

In the Panurginae such as *Panurginus, Panurgus, Perdita,* and *Psaenythia,* the pollex is reduced and does not form a tooth. *Psaenythia* has a longitudinal, median secondary ridge in the adductor interspace suggestive of that of *Colletes,* but it is not connected with the adductor ridge and is presumably of independent origin.

Protoxaea (Oxaeidae) has an inner condylar ridge similar to that of *Halictus quadricinctus.* It may be a feature of large, slender mandibles. Other striking features of the mandible of *Protoxaea* are lack of the tooth at the apex of the pollex and the weak condylar and outer ridges that are adjacent to one another distally before merging with the cap of the rutellum.

All four subfamilies of Melittidae have quite ordinary mandibles. The most unusual is *Dasypoda,* in which the mandible is unusually strongly curved and the cap of the rutellum is enormous, almost half as long as the mandible, as a result of the short grooves on the outer surface.

The Fideliidae also falls in the group showing ancestral mandibular structure. In *Fidelia* the tooth of the pollex is enormous, as large as the rutellum. In both *Fidelia* and *Neofidelia* the trimmal carina, upper carina, and the brief fimbriate line unite in a Y-shaped pattern.

In the nest-making Anthophorinae (examined in *Anthophora, Svastra, Melissodes, Centris, Diadasia, Melitoma, Exomalopsis, Tapinotaspis,* etc.), the mandibles are of the common ancestral type, with deviations in certain genera as mentioned in subsequent paragraphs.

The relations of the trimmal carina, upper carina, and fimbriate line vary widely even among bees having the generally ancestral mandibular type. In some (e.g., *Colletes*), all three structures are separated. In *Diphaglossa, Fidelia, Neofidelia, Svastra,* and some *Anthophora,* all are connected to form a Y-shaped complex and this is nearly true, also, in *Melitta* and *Andrena.* In bees such as *Anthophora, Panurginus,* and *Protoxaea,* the hairs just below the fimbriate line and trimmal carina form a single continuous row and the point where the trimmal carina stops and the fimbriate line begins is quite arbitrary. This is almost true of *Centris,* also. In *Halictus* the trimmal and upper carinae are united with one another and isolated from the fimbriate ridge. In the panurgines and *Protoxaea,* the fimbriate line is even more longitudinal than in most of the bees here discussed, a common feature among bees with slender mandibles. In *Protoxaea* the upper carina extends farther basad than usual, parallel to and almost as far as the trimmal carina. A short transverse ridge extends from the fimbriate line to a weak elevation of the upper carina.

The outer ridge in mandibles of the general ancestral type ordinarily is rather uniformly wide basally and curves upward to the vicinity of the acetabulum. In *Diphaglossa,* it is much widened basally, more than half as wide as the mandible, and almost replaces the outer interspace. In *Svastra, Anthophora* and in *Ctenocolletes,* the outer ridge has two bases, the usual upper root near the acetabulum and another, the lower root, directed toward the condyle. The lower root separates the outer groove from the outer interspace; the outer groove continues nearly to the base of the mandible and the interspace lies between the two roots of the outer ridge.

Parasitic anthophorids: Mandibles of the Nomadinae, as well as of the Melectini and Ctenioschelini of the Anthophorinae, i.e., of the parasitic Anthophoridae, are also similar to those of the ancestral type but shorter, more like those of many males. Basal parts of the condylar and outer ridges in these parasitic forms fade into the outer interspace, not reaching the base of the mandible or in *Thyreus* reaching the base, but weakly differentiated. In *Nomada* and *Ericrocis* the tooth of the pollex is absent; it is unusually large in *Thyreus* and *Melecta.* The acetabular carina is absent in *Ericrocis* and the acetabular groove is represented only by a short row of hairs in an area that is otherwise a continuum from the outer ridge to the upper carina. In *Thyreus, Melecta,* and *Ericrocis,* the trimmal carina seems continuous with the upper carina; the fimbriate line is absent but the fimbria is present, slanting away from the upper carina and in the melectines continuous with the hairs along the trimmal carina. Such mandibles are variably simplified as compared to the ancestral type; those of *Biastes* (Fig 19) are the least simplified of any parasitic anthophorid studied and would easily be placed among the mandibles of the ancestral type discussed in the preceding section.

Hylaeinae and Xeromelissinae: Other somewhat modified mandibles include those of the colletids that use preformed burrows or excavate pith, the Hylaeinae and Xeromelissinae. *Amphylaeus,* for example, has short mandibles, broad at the base and tapering apically (Fig. 5), with the cap of the rutellum much reduced by the outer interspace—outer groove which together form a broad triangle. The acetabular groove is broad, the acetabular carina absent as a sharp ridge, there being no carina, but only a space or "ridge" between the acetabular groove and the trimmal extension. The upper carina is on the inner surface of the mandible. A strong, broad secondary ridge, suggestive of that of *Colletes,* extends from the basal portion of the adductor ridge across the adductor interspace toward the distal part of the mandible. In *Hylaeus* this ridge is absent. Moreover, the trimmal carina and fimbriate line are absent; there is only a rounded surface separating the trimma from the adductor interspace. Also in *Hylaeus* the upper carina is in its usual position on the upper margin of the pollex.

Chilicola has more elongate mandibles.

An unusual feature is the extraordinarily broad acetabular groove.

Xylocopinae and Lithurginae: Bees of these subfamilies, separated according to usual classifications into two, well known families, the Anthophoridae and Megachilidae, have short mandibles, wide at the bases and commonly tridentate at the apices, because of the lower tooth of the rutellum which is the enlarged apex of the adductor ridge, in addition to the usual upper preapical tooth which is the apex of the pollex. [*Anthophora* (or *Clisodon*) *terminalis* has similar mandibular dentition although the mandible is more elongate.]

Macrogalea, Allodape, and *Ceratina* have the outer ridge narrow and at the upper margin of the large outer interspace; the ridge is carinate in *Macrogalea.* In *Macrogalea* there is a lower root of the outer ridge, a feature present also in *Manuelia.* In *Manuelia, Xylocopa,* and *Lithurge,* the outer and condylar ridges are both broad, so that the outer interspace is small. The mandibles of all these bees tend to have a deep, longitudinal depression in the middle of the apical half of the inner surface. The fimbriate line in the Xylocopinae, if recognizable, is longitudinal and along the upper margin of this depression, but in *Lithurge* it is oblique and well above the depressed area.

The ground-nesting genus *Proxylocopa* has more slender mandibles than most *Xylocopinae,* without the lower tooth of the rutellum, thus resembling the basic ancestral mandibular type. Many wood inhabiting species of *Xylocopa,* however, also lack this tooth, as shown for *X. virginica* (Fig. 24).

Megachilinae: The megachilines are remarkable for the tendency of the mandible to be broad, with the apex multidentate, especially in females. This breadth is achieved by great broadening of the area of the acetabular groove (i.e., the space between the outer ridge and the acetabular carina) to form an acetabular interspace, itself often with multiple, secondary, longitudinal ridges or rami of the outer ridge. This development, which is also seen to a lesser degree in the Apidae, is interpretable on the basis of females alone but verified from examination of males (Fig. 31), which have more slender mandibles. The acetabular groove is not particularly wide in male *Hoplitis,* for example, and the identity of the condylar and outer ridges seems clear.

The variation in the outer ridge makes one question its homology when examining species of certain other genera, especially the females. The two ridges that terminate, as in all bees that have such ridges, on the apical or first mandibular tooth (cap of the rutellum) must be the condylar and outer ridges. It is the more basal parts of the latter ridge that sometimes become confusing. In the species illustrated, the outer ridge is not complete, but it is strong and continuous in forms such as *Osmia subaustralis, subfasciata,* and *lignaria,* which have mandibles otherwise similar to those of *Hoplitis.* The basal part of the other ridge is united with the acetabular carina in all these forms. In *Noteriades* sp., however, the outer ridge has two continuous roots, the usual upper one directed toward the acetabulum and uniting with the base of the acetabular carina, and another, the median root, directed toward the abductor swelling. In *Chalicodoma exilis* and *Chelostoma fuliginosum* the upper root is broken or entirely absent, but the median root is continuous, so that the ridge runs from near the abductor swelling toward the apex of the mandible. In these forms, a secondary ridge, comparable to a similar secondary ridge in *Anthidium,* extends from near the acetabulum (where it is probably the base of the upper root of the outer ridge and is united with the acetabular carina) across the acetabular interspace toward the distal margin near the apex of the mandible. Thus there are three ridges on the outer mandibular surface leading toward the apex of the mandible instead of two. (There seems to be no justification for regarding the upper of these three ridges as the acetabular carina and all the remaining upper toothed mandibular margin as an expansion of the trimmal extension; the latter, in most bees including related megachilids, is smooth and hairless, unlike the acetabular interspace.)

In *Heriades carinata* the distal part of the outer ridge has entirely lost its normal roots and, instead, is elevated and fused near the base with the condylar ridge. The mandible is thus left with a large area lacking ridges. An independent and far more extreme loss of ridges has occurred in *Anthidiellum,* in which the outer surface is hairy almost throughout, the hairy surface curving onto the condylar interspace without an intervening ridge. The distal parts of the grooves impinging on the small cap of the rutellum are broad, flat, and minutely hairy. The inner surface of the mandible is dominated by the broad, minutely hairy concavity of the distal part of the adductor interspace. All this is suggestive of features found in some Apidae and may be related to the fact that nests of *Anthidiellum* consist entirely of plastic material (resin), like the wax, resin, or mud utilized by Apidae.

The acetabular carina and trimmal extension are distinct in most megachilines, but the carina is absent and the extension is therefore ill defined in *Anthidium* and *Callanthidium*. The trimmal carina is absent in female *Hoplitis,* but is usually present in megachilines, continuous with the fimbriate line or almost so, and both are margined on the lower side by a band or row of hairs. The fimbriate line is oblique or almost transverse, parallel to the distal margin of the mandible, in most female megachilids. In some forms, like *Hoplitis,* what appears to be the fimbriate line is angulate. In others, like *Creightonella,* there is a premarginal carina or line distal to the fimbriate line.

In *Creightonella* there is a short ridge branching from the adductor ridge and directed upward and distad. Another secondary ridge, likewise in the adductor interspace, is longitudinal and more nearly median in most megachilines.

In many megachilines (*Dianthidium, Paranthidium, Parevaspis, Euapis, Chalicodoma, Megachile frugalis* but not *albitarsis*), the distal part of the adductor ridge is provided with a strong fringe of erect hairs, as in the Meliponinae. In the same megachilines, the inner fimbria is often well developed, and in *Megachile frugalis* (not *albitarsis*) there is a conspicuous, outer premarginal fimbria.

Meliponinae and Apinae: These groups are remarkable for the lack of ridges and of the cap of the rutellum on the outer surface of the mandible. In Meliponinae a groove, perhaps in part the acetabular groove, is strongly evident. In *Apis* it is absent. When present, this oblique groove slants strongly across the mandible toward the apex (so that at least the distal part is presumably not the acetabular groove) and near the apex it branches, the lower branch going to the lower margin of the mandible, the upper continuing toward the apex. In *Meliponula* and some *Trigona* the acetabular carina is present, although weak. Except for the acetabular carina and the oblique groove (when they are present), the outer surface of the mandible is convex and rather uniformly hairy. The inner mandibular surface has a well formed adductor ridge. Distally this ridge is conspicuously fringed or hairy as in some megachilids and curves downward to form the lower margin of the mandible, but there is no condylar groove separating this margin from the rest of the outer surface of the mandible. The condylar interspace also is continuous with the outer surface of the mandible, with no intervening ridge. In workers, but not queens, of *Apis* there is a secondary, oblique carina in the adductor interspace, more or less parallel to the distal half of the adductor ridge. Such a carina is absent in Meliponinae. The fimbriate line is well developed in queens of *Apis,* less conspicuous in workers. In Meliponinae it is probably present, but its upper end is deflected distally toward the upper distal angle of the mandible. The trimmal carina is absent; the upper carina is present, forming the upper margin of the mandible distally, but does not approach the base of the mandible.

Bombinae: These large bees (see Figs. 39-42) have much more structure on the outer side of the mandible than do the Meliponini and Apinae. Thus in the Euglossini (*Eulaema, Euplusia*) there is a condylar ridge (double at the base or with an inner ridge behind the outer one as in *Halictus quadricinctus*) and an outer ridge (weak medially) delimiting an outer interspace and outer groove. Probably the distal half of the outer groove is double, with an upper and a lower branch, for an extra ridge branching from the median part of the outer ridge joins the upper part of the cap of the rutellum. Between the two branches of the outer groove is a secondary intercallary ridge. The acetabular groove is broad with a considerable space between the bottom of the groove and the acetabular carina. The acetabular carina is strong and the trimmal extension is broad and with a minutely pubescent area apically. On the inner surface, the adductor ridge is normal, the trimmal carina is absent, but the acetabular carina reaches almost to the mandibular base; it is arcuate inward subbasally and then ascends toward the acetabulum. The upper carina is present, isolated from the oblique fimbriate line. Distal to the latter is an angular transverse premarginal ridge.

In *Euglossa* the mandibles are similar to those of *Euplusia*, but the ridges and grooves on the outer surface are weak except for the acetabular groove. *Exaerete* is also similar, but the outer ridge is only incompletely divided apically by depressed islands; none of the grooves ending on the outer surface of the rutellum contain finely pubescent distal areas, as in the nonparasitic genera.

In the Bombini the condylar ridge is compound, not only basally [where the uppermost ridge of the condylar ridge system was called the basal keel by Yarrow (1954)], but also on the apical part of the mandible where the lower or inner ramus is near the lower mandibular margin, the upper well above it, terminating on the outer groove in *Psithyrus* and as a process into that groove in *Bombus*. The distal part of that groove and of the grooves above it on the outer mandibular surface (also of the condylar groove, especially in *Psithyrus*) are broad, flat, nearly reaching the distal mandibular margin, and are covered with minute pubescence. As in *Euplusia* and most other Euglossini, the outer ridge is divided distally in *Bombus*, the upper ramus (Yarrow's main keel) separating a broad, intercallary depression or groove from the broad distal part of the acetabular groove. The lower ramus is Yarrow's second keel. All the "grooves" in Bombini are so broad and flat distally as to be better described as depressed areas, and the cap of the rutellum is a mere band on the distal margin of the mandible.

DISCUSSIONS AND CONCLUSIONS

Recognition of homologous features among the ridges and grooves of mandibular surfaces is possible and these features appear to shed light on relationships among bees. A common or "basic" pattern is found in mandibles of ground-nesting groups of bees of the families Colletidae, Halictidae, Andrenidae, Oxaeidae, Melittidae, Anthophoridae, and Fideliidae. These are, for the most part, bees that make their own burrows and cells in the soil. The same pattern is widespread among sphecoid wasps and it is presumably the primitive pattern for bee mandibles. Members of these groups that nest in wood (e.g., *Callomelitta* in the Colletidae; *Megalopta*, *Augochlora* s. str., and *Lasioglossum* (*Dialictus*) *caeruleum* in the Halictidae; and *Clisodon*, a close relative of *Anthophora*, in the Anthophoridae) have similar mandibles, often modified by the acquisition of extra teeth, or not recognizably modified as in the *Lasioglossum*. Most male bees have mandibles somewhat smaller and more slender than those of females, and often with certain ridges weak or absent. Parasitic Anthophoridae (Nomadinae, Melectini, Ctenioschelini) have somewhat simplified mandibles, suggesting those of many male bees (parasitic halictids do not show this tendency).

The groups of bees listed above occupy the whole base as well as some of the top of the phylogenetic tree for the bees as presented by Michener (1944), or in modified form by Michener (1974). There are various derived types of mandibles, however, as discussed below. Thus the colletid subfamilies (Hylaeinae and Xeromelissinae) that nest in preformed cavities in the soil, wood, or stems, or perhaps excavate in pith, have rather different mandibles. Such derived mandibular types are not found, however, among bees that make subterranean burrows and earthen cells.

A significant finding is the position of the Fideliidae clearly within the basic group. There is no doubt of the similarities of fideliid larvae to those of the Megachilidae (Rozen, 1973), a relationship supported by the metasomal scopa, but the mandibular structure, independent volsellae, wing venation, and other characters make us hesitant to place the Fideliidae in the Megachilidae.

The presence of a lower tooth of the rutellum and of a deep depression on the inner mandibular surface are similarities of the anthophorid subfamily Xylocopinae (most species) and the megachilid subfamily Lithurginae. Perhaps these similarities are convergences, as suggested by the different relation of the fimbriate line to the depression in the two groups, nearly all members of which burrow in wood or pith. Other characters will have to be analyzed before the meaning of this similarity is clear. The similar dentition of *Clisodon,* a wood inhabiting genus of an otherwise ground dwelling group, shows that at least this feature can appear by convergence and may indicate little about lines of descent.

Of much interest is the finding that in the Megachilinae and to a lesser extent in the Apidae, unlike other bees, the distal part of the condylar groove or the area immediately above it is expanded to form a condylar interspace. The toothed apical margins of mandibles of these bees are therefore largely derived from the pollex of ancestral groups. It is interesting that these are the two groups which commonly carry foreign materials to the nest for construction purposes. The megachilids generally have strongly toothed mandibles for cutting, preparing, and sometimes carrying materials such as leaves, plant hairs, pebbles, and resin. The apids have weak teeth (or lack them) and more scoop shaped mandibles for handling wax, resin, mud, and the like.

In the apid subfamilies Meliponinae and Apinae, the ridges and grooves on the outer mandibular surface are largely or almost wholly absent, the surface being convex and hairy. Loss of mandibular ridges and carinae may be convergent, associated with use of relatively soft materials (wax, resin, mud) in nest making, as suggested by the relatively featureless, hairy mandibles of *Anthidiellum,* a megachilid that makes nests of resin. Absence of ridges may also be associated with minute size, suggesting that the Meliponinae and Apinae arose from minute ancestors, a view supported for the Meliponinae by their reduced wing venation, a common feature of small insects.

The Bombinae have mandibular ridges. In the illustrations and discussion we have done our best to identify them with the ridges of other families of bees. However, secondary ridges are present (not the same in the Euglossini, *Psithyrus* and *Bombus*) and it is possible that most of the ridges arose newly in Bombinae from ancestors with few ridges like the Meliponinae. In Euglossini the grooves are reasonably similar to those of other families of bees although usually minutely pubescent apically. In the Bombini, however, the "grooves," at least apically, are broad, slightly depressed, flat areas covered with short, fine hairs.

The above remarks should not be used alone as a basis for reclassification of the Apoidea. However, they should not be ignored when such a work is done. The common derived characters of the Lithurginae and Xylocopinae, and of the Megachilinae and Apidae, may well result from convergence, but if they are supported by other findings, they will require restudy of the familial classification.

The functions of the ridges and grooves

are not known, but it is reasonable to assume that they serve to strengthen the mandibular cuticle. This view is supported by the tendency for weakened and sometimes also less numerous ridges and grooves in males and parasitic female bees, which do not make nests, and in bees that construct nests of soft materials like wax and resin.

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